

OPINION

Relationship between plant hydraulic and biochemical properties derived from a steady-state coupled water and carbon transport model

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ABSTRACT

There is growing evidence that plant stomata have evolved physiological controls to satisfy the demand for CO₂ by photosynthesis while regulating water losses by leaves in a manner that does not cause cavitation in the soil–root–xylem hydraulic system. Whether the hydraulic and biochemical properties of plants evolve independently or whether they are linked at a time scale relevant to plant stand development remains uncertain. To address this question, a steady-state analytical model was developed in which supply of CO₂ via the stomata and biochemical demand for CO₂ are constrained by the balance between loss of water vapour from the leaf to the atmosphere and supply of water from the soil to the leaf. The model predicts the intercellular CO₂ concentration (C_i) for which the maximum demand for CO₂ is in equilibrium with the maximum hydraulically permissible supply of water through the soil–root–xylem system. The model was then tested at two forest stands in which simultaneous hydraulic, ecophysiological, and long-term carbon isotope discrimination measurements were available. The model formulation reproduces analytically recent findings on the sensitivity of bulk stomatal conductance (g_s) to vapour pressure deficit (D); namely, $g_s = g_{ref}(1 - m \times \ln D)$, where m is a sensitivity parameter and g_{ref} is a reference conductance defined at $D = 1$ kPa. An immediate outcome of the model is an explicit relationship between maximum carboxylation capacity (V_{cmax}) and soil–plant hydraulic properties. It is shown that this relationship is consistent with measurements reported for conifer and rain forest angiosperm species. The analytical model predicts a decline in V_{cmax} as the hydraulic capacity of the soil–root–xylem decreases with stand development or age.

Key-words: cavitation; hydraulic conductance; intercellular CO₂ concentration; maximum carboxylation capacity; photosynthesis.

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INTRODUCTION

More than two decades ago, Cowan & Farquhar (1977) argued that stomatal conductance varies so as to maximize net carbon gain while minimizing water loss to the atmosphere. Since their pioneering work, the literature on quantifying physiological controls on leaf carbon gain and hydrodynamics of water loss to the atmosphere has become quite extensive. Physiological control on leaf stomata can be quantified through a sequence of biochemical mechanisms, well described by combining the Farquhar, von Caemmerer & Berry (1980) model of photosynthesis and response of stomata to atmospheric humidity deficit (Leuning 1990, 1995; Collatz *et al.* 1991). Although these models are adequate for well-watered plants, it is clear that any complete description of stomatal conductance must include the interplay of biochemical processes in the leaves, loss of water through transpiration and the hydraulic limitations to water supply from the soil to roots and the leaf (Williams *et al.* 1996; Olliso, Carlson & Brisson 1996; Sperry *et al.* 1998; Oren *et al.* 1999; Tuzet, Perrier & Leuning 2002).

To quantify the relative importance of hydraulic and biochemical processes on annual canopy conductance, model calculations that account for the biochemical attributes of stomata can be compared to calculations that only consider plant hydraulics. Such comparisons were undertaken by Lai *et al.* (2002) in which bulk tree conductance derived from long-term sap flux measurements by Ewers *et al.* (2001a) were compared with mean annual conductance for two forest stands calculated by Lai *et al.* (2000) using a multilayer canopy model (CANVEG; Baldocchi & Meyers 1998). Lai *et al.* (2002) showed that the two approaches produced estimates of conductance close to values estimated theoretically on the basis of hydraulic limitations, calculated in Schäfer, Oren & Tenhunen (2000), and a stomatal response to water vapour pressure deficit prediction based on hydraulic theory with a broad empirical support (Oren *et al.* 1999). These predictions of stomatal conductance and behaviour is particularly striking for the CANVEG calculations because CANVEG does not consider the soil–root–xylem hydraulics (e.g. Lai *et al.* 2002) suggesting some equilibrium between the soil–plant hydraulic attributes and the

biochemical parameters of the Farquhar *et al.* (1980) model at annual time scales.

Evidence for close relationships between stomatal conductance and plant hydraulic resistance have already been demonstrated by numerous measurements (Meinzer & Grantz 1990; Saliendra, Sperry & Comstock 1995; Fuchs & Livingston 1996; Lovisolo & Schubert 1998; Bond & Kavanagh 1999; Nardini & Salleo 2000; Comstock 2000; Sperry 2000; Schäfer *et al.* 2000; Hubbard *et al.* 2001). Equally important are the theoretical findings and field experiments demonstrating that leaf water potential cannot drop below a critical value (Tyree & Sperry 1988, 1989; Sperry *et al.* 1998; Ewers, Oren & Sperry 2000; Hacke *et al.* 2000; Hubbard *et al.* 2001). Should this occur, cavitation and loss of hydraulic conductivity rapidly follow in the soil–root–xylem system, leading to desiccation and death of the leaves.

It is also recognized that plant hydraulic and ecophysiological properties are not static but evolve with plant age and growth conditions (Yoder *et al.* 1991; Saliendra *et al.* 1995; Hubbard, Bond & Ryan 1999; Schäfer *et al.* 2000; Meinzer, Clearwater & Goldstein 2001). Given the connection between soil–root–xylem hydraulics, leaf stomatal conductance, and carbon gain, it may be argued that the key hydraulic and biochemical properties of plants must be related at some time scale relevant to stand development, although such a relationship has hitherto not been explored. Experimentally, one study has reported a strong correlation between leaf area-specific stem hydraulic conductivity and maximum photosynthetic capacity (Brodribb & Feild 2000), leading the authors to conclude that the maximum photosynthetic capacity of leaves and plant hydraulic conductivity do not operate independently.

In this study, we go further and suggest that photosynthetic parameters adjust so that the maximum biochemical demand for carbon uptake is in *equilibrium* with the maximum carbon gain permissible by the soil–root–xylem hydraulics on time scales relevant to stand development. We show that such an *equilibrium hypothesis* permits estimation of long-term, mean intercellular concentration (C_i), and hence, can be indirectly tested with carbon isotope discrimination measurements (e.g. Farquhar, Ehleringer &

Hubick 1989; Ehleringer 1993; Ehleringer & Cerling 1995). An outcome of the equilibrium hypothesis is an analytic relationship between V_{cmax} and the maximum root-to-leaf hydraulic conductance.

THEORY

Hydraulic limits on transpiration

The transport of water from the soil reservoir to the leaf is given by

$$J_w = \frac{\psi_s - \psi_e}{r_{sr} + r_{re}} \quad (1)$$

where J_w is the water flux from the soil to the leaf, ψ_s and ψ_e are the water potentials in the soil and leaf, respectively, and r_{sr} and r_{re} are the hydraulic resistance values to the flow from the soil to the root and from the root to the leaf, respectively (Fig. 1). In unsaturated soils, r_{sr} is primarily controlled by the hydraulic properties of the soil and is given by

$$r_{sr} = \frac{L_{sr}}{K(\theta)}, \quad (2a)$$

where $K(\theta)$ is the soil hydraulic conductivity function, θ is the soil moisture content, and L_{sr} is the effective distance travelled by a water molecule from the soil to the root surface. The hydraulic conductivity and soil water potential can both be estimated from θ using the Clapp & Hornberger (1978) relationships, given by

$$K(\theta) = K_{sat} \left(\frac{\theta}{\theta_{sat}} \right)^{2b+3} \quad (2b)$$

$$\psi_s(\theta) = \psi_{sat} \left(\frac{\theta}{\theta_{sat}} \right)^{-b}$$

where K_{sat} and ψ_{sat} are the soil hydraulic conductivity and soil water potential near field saturation (defined at θ_{sat}) and b is an empirical parameter that varies with soil texture and pore-space structure. An order of magnitude estimate of L_{sr} may be obtained from the root-zone depth (L_r) and root area index (R_{AI}) using a simplified cylinder model for root surface area.

$$L_{sr} = \pi L_r (R_{AI})^{-1/2} \quad (2c)$$

The hydraulic approach of Sperry *et al.* (1998) suggests that r_{re} is strongly dependent on ψ_e below a critical threshold value. The simplest analytical function which illustrates the key attributes of the variation of r_{re} with water potential is the ramp function given by

$$\frac{1}{r_{re}} = \begin{cases} G_{re,max} & \text{if } \psi_e > \psi_{tl} \\ G_{re,max} \times \left(\frac{\psi_e - \psi_{xl}}{\psi_{tl} - \psi_{xl}} \right) & \text{if } \psi_{xl} < \psi_e < \psi_{tl} \\ 0 & \text{if } \psi_e < \psi_{xl} \end{cases} \quad (3)$$

where $G_{re,max}$ is the maximum root-to-leaf hydraulic conductance, ψ_{tl} is the threshold potential at which the root-to-leaf hydraulic conductivity begins to decline with decreasing potential, and ψ_{xl} is the potential at which the root-to-

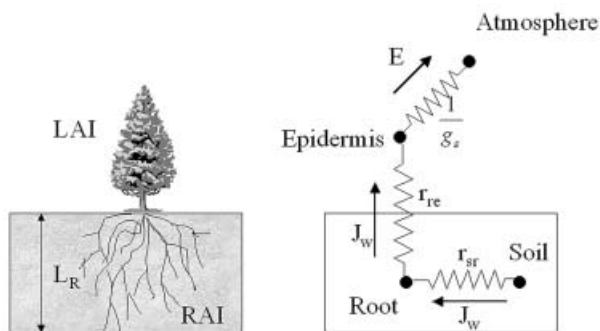


Figure 1. Schematic diagram of the resistances to water flow from the soil to the atmosphere through the root–leaf pathway. Steady-state conditions require that water flux from the soil to the leaf (J_w) balances the water loss to the atmosphere (E).

leaf hydraulic conductivity function becomes negligible. It should be pointed out that ψ_{tl} and ψ_{sl} represent whole-plant hydraulic parameters but are rarely measured at such a scale. Equations 1–3 describe the hydraulic capacity of the soil–root–xylem system to supply water to the leaf, J_w .

Atmospheric-demand limits on transpiration

Using a big-leaf representation of the canopy (Fig. 1), water loss from the big leaf to the atmosphere (E) is given by

$$E = 1.6g_s \times D_s \quad (4)$$

where g_s is the bulk stomatal conductance to CO_2 , and D_s is the vapour pressure difference between the plant intercellular space and the atmosphere (assuming boundary layer conductance is much larger than stomatal conductance). Net photosynthesis (A_n) and g_s are related by

$$g_s = \frac{A_n}{C_s - C_i} \quad (5)$$

where C_s is the leaf surface CO_2 concentration. Substituting Eqn 5 in Eqn 4, we obtain

$$E = \frac{1.6A_n D_s}{C_s - C_i} \quad (6)$$

Steady-state water transport and hydraulic limitations on photosynthesis

For a steady-state system (e.g. Fig. 1), the water supply from the soil–root system and atmospheric demand are in balance (i.e. $J_w = E$) leading to

$$A_n = \left(\frac{\psi_s - \psi_e}{r_{sr} + r_{re}} \right) \times \frac{C_s - C_i}{1.6D_s} \quad (7)$$

The steady-state water balance results in a linear relationship between A_n and C_i in which the slope and intercept are dependent on soil water potential (ψ_s), leaf potential (ψ_e), and atmospheric driving force (D_s). It is possible to use Eqn 7 to assess the controls on the A_n – C_i curve for hydraulically limited plants.

As shown by Sperry (2000), plants typically operate at a value of ψ_e which is above or near the critical potential at which cavitation commences. Hence, at $\psi_e \approx \psi_{tl}$ the plant achieves the maximum ‘permissible’ potential gradient that avoids significant loss of hydraulic conductivity in the root–xylem system. In a first-order analysis, and to retain tractability of the analytical derivation, we set $\psi_e \approx \psi_{tl}$, $r_{re} \approx \frac{1}{G_{re,max}}$ (i.e. constant) so that Eqn 7 permits estimation of the maximum ‘hydraulically permissible’ A_n without cavitation of the root or stem xylem. That is,

$A_n = \gamma^* \times (C_a - C_i)$; where

$$\gamma^*(D, \theta) = \left(\frac{1}{1.6D} \times \frac{\psi_s(\theta) - \psi_{tl}}{\frac{L_{sr}}{K(\theta)} + \frac{1}{G_{re,max}}} \right) \quad (8)$$

for $D > 0$. We have assumed $D_s \approx D$ and $C_s \approx C_a$ to obtain ‘first order’ estimates of γ^* from long-term atmospheric

drivers, where D is the atmospheric vapour pressure deficit and C_a is the atmospheric CO_2 concentration. In short, for specified soil moisture (or ψ_s) and atmospheric forcing (D), the slope of the A_n – C_i curve ($= \gamma^*$ or the bulk stomatal conductance of the big leaf to CO_2) is controlled by the hydraulic properties of the soil–root–xylem system. We define the stomatal conductance per unit leaf area as $\gamma = \gamma^*/L_{AI}$, where L_{AI} is the leaf area index. We also distinguish between γ^* , the approximate conductance of the big leaf subject to all the hydraulic approximations in the soil–plant–atmosphere system, and g_s , which is the exact conductance.

Biochemical limitations on photosynthesis

Equation 8 represents the maximum A_n resulting from the maximum hydraulically permissible supply of water at a given soil potential and for specified soil–root–xylem hydraulic properties. The biochemical demand for CO_2 uptake also leads to an A_n – C_i curve described by the Farquhar *et al.* (1980) photosynthesis-biochemical model of C_3 plants and whose canonical form is given by

$$A_n = \frac{\alpha_1(C_i - \Gamma^*)}{C_i + \alpha_2} - R_d, \quad (9)$$

where $\alpha_1 = \alpha_p Q_p e_m$ and $\alpha_2 = 2\Gamma^*$ for light-limited photosynthesis, or $\alpha_1 = V_{cmax}$ and $\alpha_2 = k_c \left(1 + \frac{o_i}{k_o} \right)$ for photosynthesis limited by Rubisco activity, α_p is the leaf absorptivity for photosynthetically active radiance Q_p , e_m is maximum quantum efficiency, Γ^* is the compensation point for CO_2 in the absence of dark respiration, V_{cmax} is the maximum carboxylation capacity of Rubisco, k_c and k_o are the Michaelis constants for CO_2 fixation and O_2 inhibition with respect to CO_2 , and o_i is the oxygen concentration. The biochemical parameters vary with temperature (T) as described in Campbell & Norman (1998) and Leuning (1995, 1997, 2002).

Steady-state photosynthesis model

We consider the ‘steady-state’ C_i resulting from both hydraulic and biochemical limits on the A_n – C_i curves. Again, in a first-order analysis, we neglect R_d relative to A_n and match Eqn 8 to Eqn 9 which yields a quadratic equation in C_i :

$$\kappa_1 C_i^2 + \kappa_2 C_i + \kappa_3 = 0$$

$$\kappa_1 = -\gamma$$

$$\kappa_2 = \gamma(C_a - \alpha_2) - \alpha_1$$

$$\kappa_3 = \alpha_2 \gamma C_a + \alpha_1 \Gamma^*$$

whose solution is given by

$$C_i = \frac{-\kappa_1 \pm \sqrt{\kappa_2^2 - 4\kappa_1 \kappa_3}}{2\kappa_1} \quad (10)$$

The C_i in Eqn 10 is the result of a balance between biochemical (enzyme kinetics) and hydraulically controlled

photosynthesis. The corresponding leaf A_n and g_s can be computed from Eqns 9 and 5. The solution in Eqn 10 has two roots, one where $C_i > C_a$, corresponding to a negative E , and the other where $C_i < C_a$, corresponding to a positive E . The second of these two roots must be chosen.

We restate that Eqn 10 is only approximate and subject to numerous simplifications, listed below:

- 1 The model is implicitly a ‘big-leaf’ and treats the entire plant as a single photosynthetic object. As such, its validity is proportional to the validity of the assumptions that underlie the big-leaf simplification. Similar scaling assumptions apply to soil–root resistances in which the roots are treated as cylinders perfectly connected to the soil water. Furthermore, the computed L_{sr} is only an order of magnitude estimate and is likely to vary appreciably with root diameter and root length density (Campbell 1991).
- 2 ψ_e is constant and near its permissible limit at all times

of the day and over the entire duration of stand development.

- 3 Boundary layer resistance is assumed negligible compared to the stomatal resistance.
- 4 Dark respiration is assumed negligible relative to gross photosynthesis.
- 5 CO₂-water vapour diffusive interference (i.e. the ‘ternary effects’) is ignored.

Despite these numerous simplifications, which lead to $g_s \approx \gamma^*$, this equation captures analytically the major factors controlling long-term C_i , including basic attributes of plants ($G_{se,max}$, ψ_{tl} , L_{AI} , V_{cmax} , Γ^*), soil type (ψ_{sat} , K_{sat} , b , θ_s), soil water status (θ), the humidity deficit (i.e. D_s) at the leaf surface which we assume to be well approximated by the atmospheric vapour pressure deficit D , and CO₂ concentration. For example, we show in Fig. 2 how C_i/C_a varies with soil water status (θ) and atmospheric humidity deficit (D_s) for two contrasting soil types (sand and clay) and for two

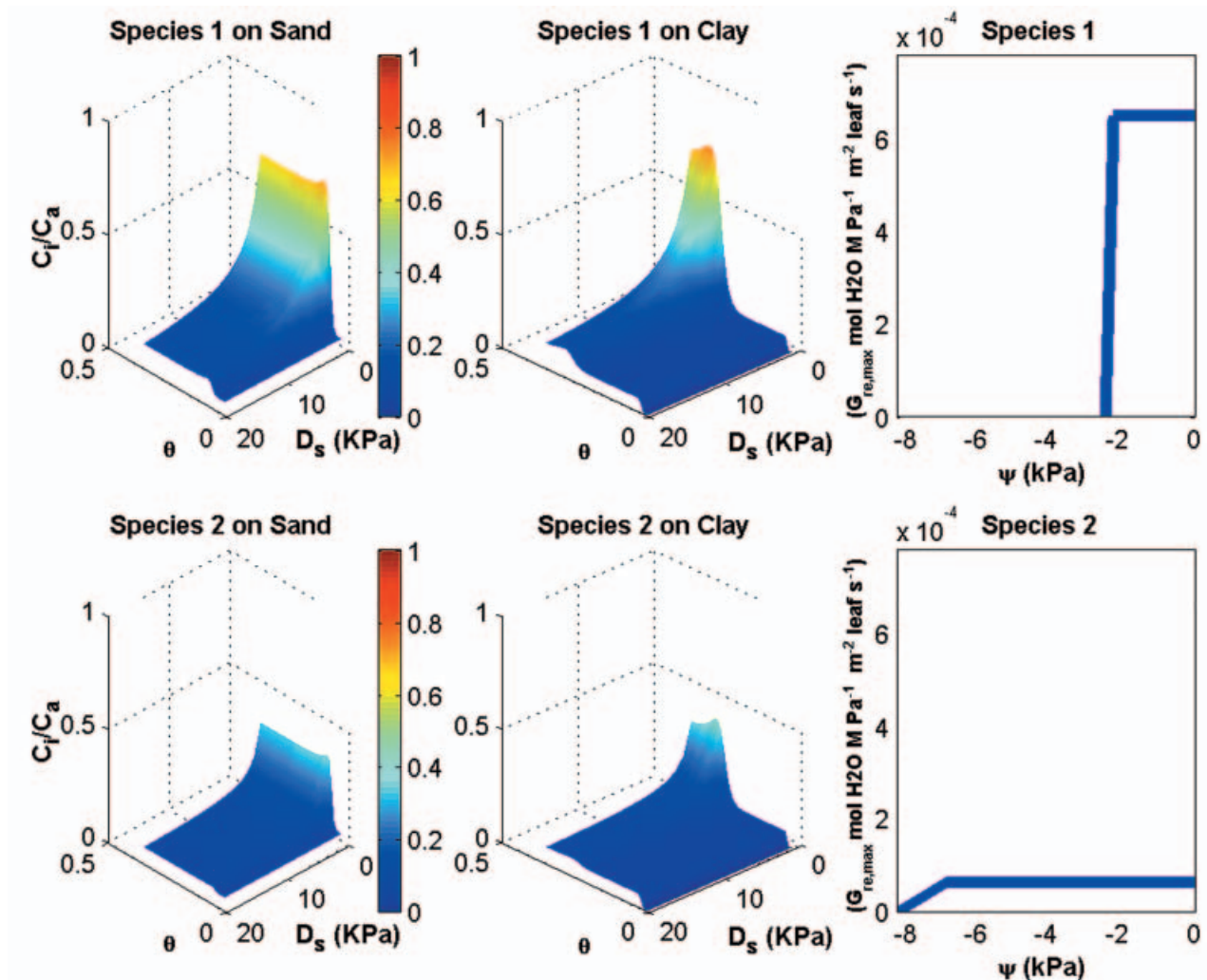


Figure 2. Variation of C_i/C_a with soil moisture (θ) and atmospheric forcing (D) for two soil types (sand and clay) and two species having different vulnerability curves (also shown). As illustration, the vulnerability curve (right panels) for species 1 trees has high $G_{re,max}$ but low ψ_{tl} whereas that of species 2 has low $G_{re,max}$ and high ψ_{tl} (see Table 1).

Parameters		
Soil ^a		
Texture	Clay	Sand
K_{sat} (m s ⁻¹)	1.3×10^{-6}	176×10^{-6}
ψ_{sat} (m)	0.065	0.121
b	11.4	4.05
θ_{sat}	0.49	0.40
Root		
L_d (m)		0.30
R_{AI} (m ² root m ⁻² ground)		5.46
Plant		
Plant type	Species 1	Species 2
L_{AI} (m ² leaf m ⁻² ground)		3.0
ψ_{li} (MPa)	-2.31	-7.00
$G_{\text{re,max}}$ (mol H ₂ O MPa ⁻¹ m ⁻² leaf s ⁻¹)	0.65×10^{-3}	0.65×10^{-4}
$k_{\text{c},25}$ ($\mu\text{mol m}^{-2}$ leaf s ⁻¹)		300
$k_{\text{o},25}$ ($\mu\text{mol m}^{-2}$ leaf s ⁻¹)		300
[O ₂] (mmol m ⁻² leaf s ⁻¹)		210
Γ^* ($\mu\text{mol m}^{-2}$ leaf s ⁻¹)		36.9
$V_{\text{cmax},25}$ ($\mu\text{mol m}^{-2}$ leaf s ⁻¹)		60

Table 1. Hydraulic and ecophysiological parameters assumed in the model calculations of Fig. 2. In this example, only the soil and some of the plant hydraulic attributes were parameterized with different values

^aFrom typical clay and sand after Clapp & Hornberger (1978).

tree species with different xylem vulnerability curves (species 1 – high $G_{\text{se,max}}$ and small negative ψ_{li} , and species 2 – low $G_{\text{se,max}}$ and more negative ψ_{li}). The numerical values of the parameters used in this hypothetical example are summarized in Table 1.

Intercellular CO₂ concentrations in Fig. 2, modelled based on the arbitrary set of parameter values shown in Table 1, clearly depend on soil type, atmospheric humidity deficit and leaf physiochemical characteristics. The model shows that C_i/C_a for species 2 is expected to be less than for species 1 at high values of θ and low D and that for species 1, which is more susceptible to cavitation than species 2, C_i/C_a decreases rapidly with θ at any value of D . Note that the low C_i/C_a shown in Fig. 2 reflects the asymptotic limits for the range in soil water availability and atmospheric demand for water vapour, and not aimed to demonstrate the ratio under realistic climate conditions. We emphasize that for short-term duration (~ hours or even days), it is unlikely that the biochemical demand for CO₂ is in exact balance with the hydraulic limitations on its supply. Furthermore, it is unlikely that ψ_c is constant and near its permissible limit at all times of the day and over the entire duration of stand development. However, it is plausible that the hydraulic and ecophysiological properties adjust in concert over the course of the stand development (~ year) so that the stand achieves some equilibrium between the maximum biochemical demand for carbon assimilation and hydraulic limitations imposed on its supply.

We selected C_i as the ‘state variable’ in the evaluation of the proposed equilibrium for three reasons.

1 Long-term mean values of C_i are now available based on carbon isotopes discrimination techniques (e.g. Farquhar *et al.* 1989; Ehleringer 1993);

2 The long-term C_i/C_a is a dimensionless number constrained between 0.5 and 0.9 for several C₃ species (e.g. Wong, Cowan & Farquhar 1979; Norman 1982; Leuning 1995; Katul, Ellsworth & Lai 2000)

3 The value of C_i can be readily interpreted as the operating point between the demand for CO₂ by photosynthesis and the maximum conductance permissible by soil–plant hydraulics at a given C_a , D and θ . Figure 3 illustrates such an interpretation with the demand curve for CO₂ computed from Eqn 9 and the stomatal conductance computed from Eqn 8. The fixed point on the abscissa is the external CO₂ concentration, C_a , and the straight lines geometrically represent $-\gamma$. The operating point of the leaves (A_n , C_i) is given by the intersection of the biochemical demand curve and the supply lines. This figure demonstrates that C_i and its sensitivity to D can vary with soil type even if all other parameters, including photosynthetic capacity and soil moisture, are held constant. Thus at $\theta = 0.3$ and at any given humidity deficit, g_s , A and C_i are predicted to be higher for plants growing in clay soils than in sand. The difference in this hypothetical example arises because $\psi(\theta)$ and $K(\theta)$ (and hence r_{sr}) differ for sand and clay at the same soil water content.

RESULTS

Model testing

The steady-state model of photosynthesis and plant hydraulics was tested based on data from two forest stands for which we have measurements of the necessary hydraulic and ecophysiological properties and long-term values of C_i/C_a from carbon isotope discrimination methods. With C_i/C_a predicted, the model can be extended to predict the long-

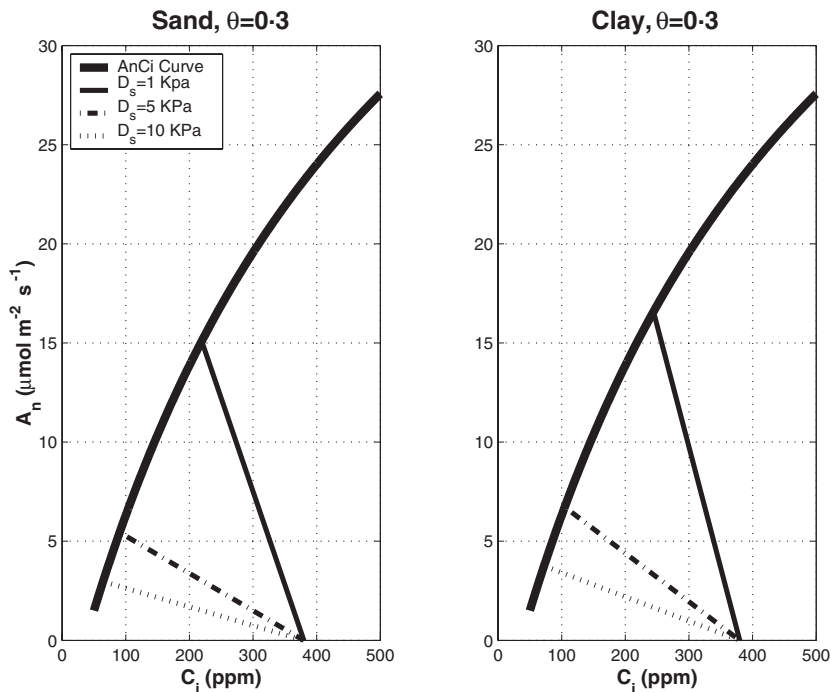


Figure 3. Illustration of the equilibrium C_i as a balance between the demand function

$$A_n = \frac{V_{\text{cmax}}(C_i - \Gamma^*)}{C_i + \alpha_2}$$

and the conductance $\gamma^*(D, \theta)$ set by the hydraulic properties and vapour pressure deficit (D) assuming well-watered conditions ($\theta = 0.3$). The physiological and plant hydraulic parameters of the Duke Forest site, shown in Table 2, are used. For soil hydraulic properties, parameter values from Clapp & Hornberger (1978) are used.

term bulk canopy conductance. We note that the model calculations do not assume *a priori* any particular conductance response to environmental variables and that the formulation strictly accounts for the resistance in the flow path. Hence, another indirect test of the steady-state model is reproducing the general behaviour of stomata in response to changing D already reported from detailed calculations of plant hydraulics and field measurements (Oren *et al.* 1999). As a final test of the equilibrium hypothesis, we will evaluate the qualitative consistency of the predicted relationship between V_{cmax} and γ with observed patterns of V_{cmax} for different biomes varying in age and L_{AI} (both leading to predictable changes in γ).

Duke Forest and SETRES study sites

The two study sites are *Pinus taeda* L. tree plantations situated in North Carolina, USA. The first is a 15-year-old-plantation (in 1998) on a clay loam soil at the Duke Forest near Durham (35°58' N, 79°8' W) and is the same stand used for a free air CO₂ enrichment (FACE) project (Ellsworth 1999, 2000) and an *AmeriFlux* site (Katul *et al.* 1999). The second is a sandy soil site with a 14-year-old plantation at the South-east Tree Research and Education Site (SETRES) in the sandhills of south-central North Carolina (34°48' N, 79°12' W; Albaugh *et al.* 1998; King *et al.* 1999; Hacke *et al.* 2000). Annual precipitation at both sites is, on average, about 1200 mm. Details of the hydraulic and ecophysiological parameters for each site are summarized in Table 2, and the variation of daytime D (defined from local sunrise to local sunset) is shown in Fig. 4. We note that for these two stands, approximating D_s by D is shown to be reasonable by Ewers & Oren (2000).

Using Eqn 10 we estimate C_i/C_a for both sites and for a wide range of θ and two values of D (Fig. 4). The mean values of C_i/C_a estimated from carbon isotope analysis of leaves for each site are also plotted as a function of mean soil moisture content in Fig. 4. Details of the carbon isotope analysis for SETRES and Duke Forest are presented in Lai *et al.* (2002), Katul *et al.* (2000), and Ellsworth (1999). Briefly, the carbon isotope ratio was determined on sun-type needles collected from the upper crown of eight trees during the growing season. The monthly daytime D ranges from a minimum of 0.4 kPa (winter) to 1.5 kPa (summer) for both forests. The mean annual daytime D value is about 0.8 kPa (Schäfer *et al.* 2002). The corresponding mean θ is about 0.08 for SETRES (Ewers *et al.* 2001a, b) and about 0.20 for the Duke Forest (Schäfer *et al.* 2002). The model predicts that C_i/C_a remains relatively constant at high moisture content but drops rapidly as the soil dries, with the moisture content at which the decrease commences being dependent on soil type. The C_i/C_a patterns modelled are similar to the patterns in reference canopy conductance found at the two sites (Oren *et al.* 1998; Hacke *et al.* 2000; Ewers *et al.* 2001a, b). Mean values of C_i/C_a estimated using carbon isotopes also showed good agreement with model calculations when $D = 0.8$ kPa.

Another interesting point in Fig. 4 is the relationship between the value of C_i/C_a and the soil moisture content at which bulk canopy conductance declines. From leaf porometry measurements in summer-time at both sites, we use the minimum recorded C_i/C_a (~0.5) to estimate this soil moisture. The resulting estimates for SETRES and Duke Forest are $\theta = 0.055$ and $\theta = 0.19$, respectively (again using $D = 0.8$ kPa). From sapflux measurements, Oren *et al.* (1998) reported a threshold $\theta = 0.20$ at which bulk canopy

Parameters	Duke Forest	SETRES	Reference
Soil			
Texture	Clay loam	Sand	1, 2
K_{sat} (m s^{-1})	3.39×10^{-6}	19.4×10^{-6}	1, 2
ψ_{sat} (m)	0.117	0.065	1, 2
b	4.95	2.56	1, 2
θ_{sat}	0.55	0.40	1, 2
Root			
L_{d} (m)	0.30	~1.0	1, 2
R_{AI} ($\text{m}^2 \text{ root m}^{-2} \text{ ground}$)	5.46	14.19	2
Plant			
L_{AI} ($\text{m}^2 \text{ leaf m}^{-2} \text{ ground}$)	3.8	1.8	3, 2
C_i/C_a	0.67	0.70	4, 5
ψ_{tl} (MPa)	-2.31	-1.61	2
$G_{\text{re,max}}$ ($\text{mol H}_2\text{O MPa}^{-1} \text{ m}^{-2} \text{ leaf s}^{-1}$)	0.65×10^{-3}	1.07×10^{-3}	2
$k_{\text{c},25}$ ($\mu\text{mol m}^{-2} \text{ leaf s}^{-1}$)		300	6
$k_{\text{o},25}$ ($\mu\text{mol m}^{-2} \text{ leaf s}^{-1}$)		300	6
$[\text{O}_2]$ ($\text{mmol m}^{-2} \text{ leaf s}^{-1}$)		210	6
Γ^* ($\mu\text{mol m}^{-2} \text{ leaf s}^{-1}$)		36.9	4
$V_{\text{cmax},25}$ ($\mu\text{mol m}^{-2} \text{ leaf s}^{-1}$)	60	85	7, 5

References: 1, Oren *et al.* (1998); 2, Hacke *et al.* (2000); 3, Ellsworth (1999); 4, Katul *et al.* (2000); 5, Lai *et al.* (2002); 6, Campbell & Norman (1998); 7, Lai *et al.* (2000).

conductance of the Duke Forest *P. taeda* trees are primarily controlled by θ . Similarly, Ewers *et al.* (2001b) reported a threshold of $\theta = 0.049$ at which bulk canopy conductance measured using sap fluxes in SETRES rapidly declines with θ . Both soil moisture threshold limits are consistent with the analytical model calculations.

Modelled conductance variation with D

We assessed the consistency of the equilibrium model with the sensitivity of stomatal conductance to D found by Oren *et al.* (1999), given by $g_s = g_{\text{ref}}(1 - m \times \ln D)$, where g_{ref} is a reference conductance defined at $D = 1$ kPa and m is a sensitivity parameter (Oren *et al.* 1999). Such a relationship can be derived if it is assumed that the response of g_s to D is due to stomatal regulation of plant water potential above the value in which catastrophic cavitation may be initiated (Oren *et al.* 1999; Tuzet *et al.* 2002). Based on this approach, higher stomatal conductance at a reference D leads to a proportional increased sensitivity of stomatal conductance to D to preserve the hydraulic integrity of the flow path.

Thus, when the conductance is expressed as $g_s = g_{\text{ref}}(1 - m \times \ln D)$, a near-constant value of $m \in [0.53-0.60]$ emerges. The value of m computed in Oren *et al.* (1999) compares well with values obtained from whole-tree and leaf conductance measurements made on a wide range of non-woody and woody species, of different xylem types, in ecosystems representing the range from tropical to boreal (Black & Squire 1979; Oren *et al.* 1999, 2001; Ewers *et al.* 2000, 2001a, b; Schäfer *et al.* 2000; Oren & Pataki 2001).

These findings (including m) can be reproduced analytically by noting that Eqn 8 can be expressed as

$$g_s = \frac{f(V_{\text{cmax}}, \theta, L_{\text{max}}, \psi_{\text{tl}}, \dots)}{D},$$

so that at $D = 1$ kPa $g_s = g_{\text{ref}} = f(\bullet)$, where $f(\bullet)$ is a function given by Eqn 8 for $D = 1$ kPa. At first glance, the two formulations appear inconsistent as the equilibrium model predicts a g_s proportional to D^{-1} while the g_s model tested in Oren *et al.* (1999) predicts g_s proportional to $1 - m \times \ln(D)$. This apparent discrepancy can be rectified if we note that $1/D \approx 1 - 0.5 \ln(D)$ for D varying between 1 and 5 kPa. It is for this reason that the value of m in the Oren *et al.* (1999) model must be a near constant close to 0.5 and appears sensitive to the D range used, as well as the other factors in Eqn 8.

DISCUSSION

Thus far, we have shown that the steady-state photosynthesis and hydraulic conductance model produces realistic estimates of long-term C_i consistent with carbon isotope discrimination measurements at two sites. To achieve our stated goal, an analytic relationship between the leaf ecophysiological and soil-plant hydraulic properties must be established.

We express V_{cmax} as a function of γ^* , L_{AI} , and long-term C_i/C_a ($= \xi_c$) by combining Eqns 8 and 9 to give

$$V_{\text{cmax}} = C_a \times \frac{\gamma^*}{L_{\text{AI}}} \times \left(\frac{(1 - \xi_c) \times \left(\xi_c + \frac{\alpha_2}{C_a} \right)}{\xi_c} \right) \quad (11a)$$

where Γ^*/c_a is neglected (when compared to unity, it is less than 10%). Also, α_2/C_a is approximately constant $\sim (510/$

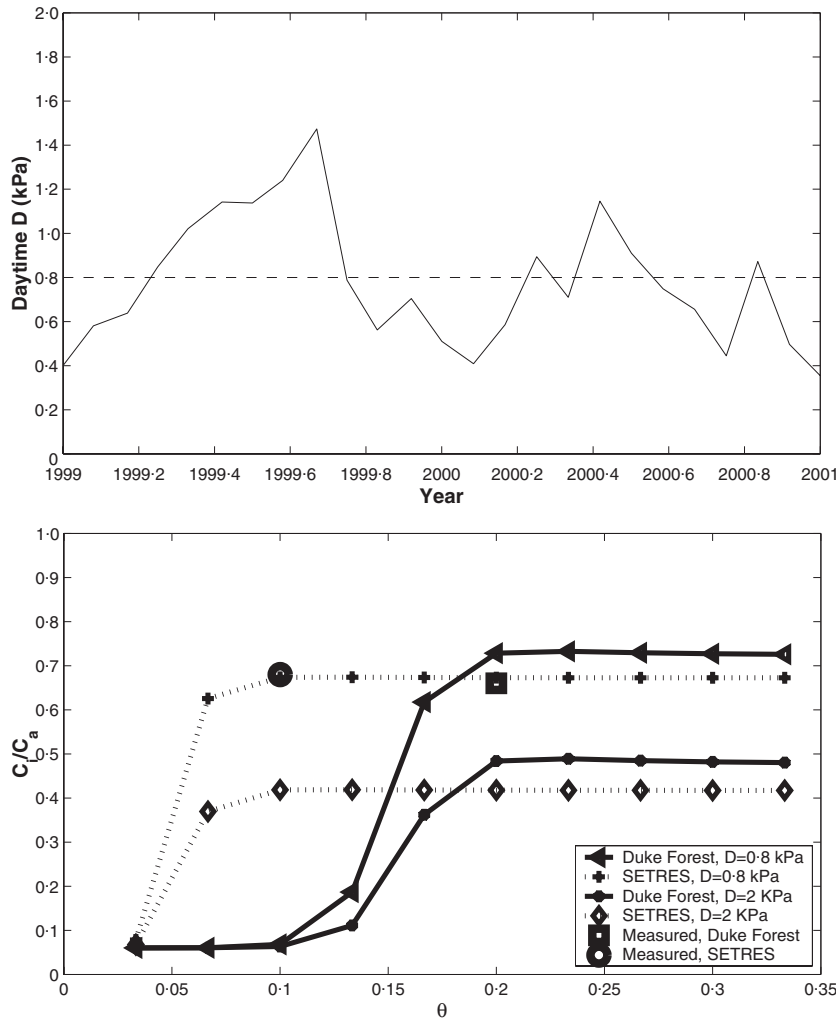


Figure 4. Top: Variation of the daytime D at the Duke pine forest. The long-term mean value ($= 0.8$ kPa) is also shown. Bottom: Modelled C_i/C_a as a function of θ and typical mean annual daytime $D = 0.8$ kPa for SETRES and Duke Forest. The calculations of C_i/C_a as a function of θ for $D = 2$ kPa are also shown for reference. The parameter values in Table 2 were used in the model calculations. The measured C_i/C_a from carbon isotopes at both sites are also shown.

380). For a wide range of species, long-term ξ_c is also restricted to a limited range (between 0.50 and 0.9 as in Leuning 1995; Katul *et al.* 2000). Hence, we find that an explicit relationship between ecophysiological and hydraulic attributes emerges, given by

$$V_{\text{cmax}} = \frac{K(\theta)G_{\text{re,max}}}{L_{\text{sr}}G_{\text{re,max}} + K(\theta)} \frac{1}{1.6D} \times (\psi_s(\theta) - \psi_{\text{tl}}) \times \left(\frac{C_a}{L_{\text{AI}}} \frac{(1 - \xi_c) \times \left(\xi_c + \frac{\alpha_2}{C_a} \right)}{\xi_c} \right) \quad (11b)$$

In the above derivation, we have assumed that $\alpha_1 = V_{\text{cmax}}$. This derivation could be repeated with $\alpha_1 = \alpha_p Q_p e_m$ and $\alpha_2 = 2\Gamma^*$ rather than $\alpha_1 = V_{\text{cmax}}$ and $\alpha_2 = k_c \left(1 + \frac{\alpha_1}{k_o} \right)$ if electron transport limits photosynthesis. From Eqn 11b, when $K(\theta) \gg L_{\text{sr}}G_{\text{re,max}}$, a linear relationship between V_{cmax} and $G_{\text{re,max}}$ emerges assuming all other parameters are held constant. Such a linear relationship between photosynthetic capacity and plant hydraulic conductivity was observed by Brodrribb & Feild (2000; their Fig. 2) using a combination

of chlorophyll fluorescence and hydraulic analysis on seven conifers and 16 angiosperm rainforest species in New Caledonia and Tasmania.

In Fig. 5, we show the predicted variation of V_{cmax} with $G_{\text{re,max}}$ for $D = 1$ kPa, $\psi_{\text{tl}} \approx -0.5$ MPa (determined by us assuming the leaf pressure in Fig. 3 of Brodrribb and Feild is near ψ_{tl}), and an assumed $L_{\text{AI}} = 3$, $C_a = 380$ p.p.m., and $\xi_c = 0.7$, and for a wide range of soil moisture conditions. In these calculations, the soil type was assumed to be sandy clay loam (for illustration) whose hydraulic properties are given by Clapp & Hornberger (1978). For well-watered conditions ($\theta > 0.3$), we show that V_{cmax} increases linearly with $G_{\text{re,max}}$ with a slope not sensitive to θ , compatible with the observations by Brodrribb & Feild (2000; annual precipitation in New Caledonia and Tasmania exceeds 1800 mm). However, it is not possible to compare directly the results of our model with those of Brodrribb & Feild (2000) because they reported the mean quantum yield of photosystem II electron transport (ϕ_{PSII}) and provided no information about soil type, L_{AI} , and ξ_c . However, we do note that their ϕ_{PSII} varied by a factor of 7 and our computed V_{cmax} varied by a factor of 8 for the same range in $G_{\text{re,max}}$. The model in

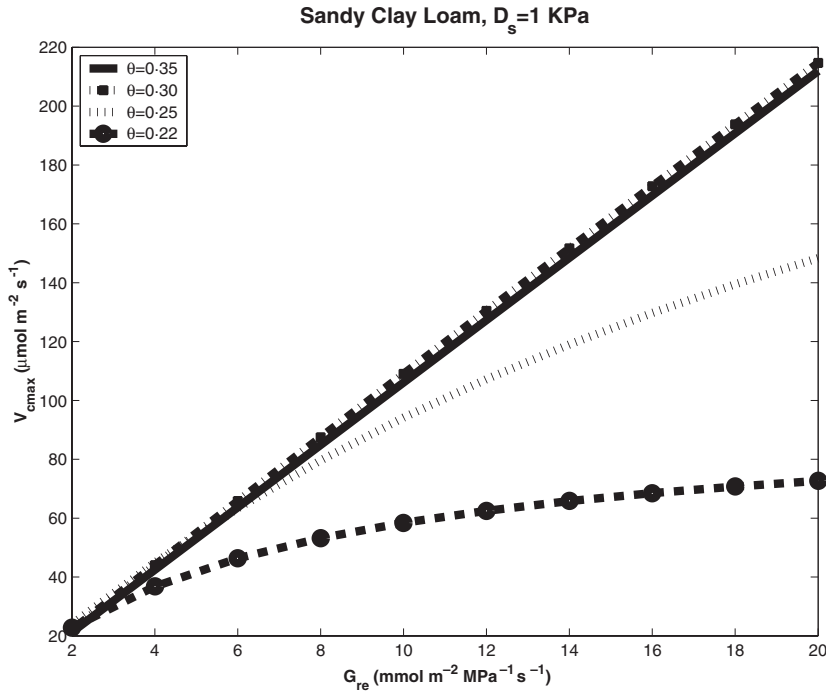


Figure 5. The variation of V_{cmax} with θ and $G_{re,max}$ for the range of $G_{re,max}$ reported in Brodrigg & Feild (2000) using Eqn 11b, with $\psi_{fl} = -0.5$ MPa (from Brodrigg & Feild 2000), $\xi_c = 0.7$, $D = 1$ kPa, and for a sandy-clay loam whose hydraulic properties are given in Clapp & Hornberger (1978). For wet conditions, Brodrigg & Feild (2000) reported a linear dependence between mean ϕ_{psII} and specific xylem conductivity with a squared correlation coefficient (r^2) = 0.74.

Eqn 11b goes further to suggest that when θ decreases, $K(\theta)$ is no longer large when compared with $G_{re,max}$ resulting in a non-linear relationship between V_{cmax} and $G_{re,max}$ (Fig. 5). There is likely to be a curvilinear relationship between V_{cmax} and $G_{re,max}$ in drier climates with the degree of non-linearity strongly dependent on soil type and soil moisture content.

Another consequence of the equilibrium model with an approximately constant ξ_c is that the ratio of V_{cmax} between two different species or for the same species at different developmental age is primarily driven by

$$\frac{V_{cmax}^{(1)}}{V_{cmax}^{(2)}} \approx \frac{L_{AI}^{(2)}}{L_{AI}^{(1)}} \times \frac{\gamma^{*(1)}}{\gamma^{*(2)}} \quad (12)$$

So, it is possible to express Eqn 12 in terms of quantities that may be easier to model or estimate such as L_{AI} and $g_{s,max}$:

$$\frac{V_{cmax}^{(1)}}{V_{cmax}^{(2)}} \approx \frac{L_{AI}^{(2)}}{L_{AI}^{(1)}} \times \frac{g_{s,max}^{(1)}}{g_{s,max}^{(2)}} \quad (13)$$

We note that Eqn 13 also follows from Eqns 5 and 9 for Rubisco-limited photosynthesis at constant ξ_c . The latter approximation appears to be valid across a wide range of species as demonstrated by Schultze *et al.* (1994), who reported a linear relationship between maximum bulk conductance and maximum photosynthetic capacity per unit ground area for tropical, temperate deciduous broad-leaved forests, temperate evergreen broad-leaved forests, tropical forest, and herbaceous tundra with an approximate slope consistent with $\xi_c = 0.82$.

To further illustrate the applicability of Eqn 13, we consider the fertilization experiment at SETRES-II described in Lai *et al.* (2002) in which V_{cmax} and L_{AI} were measured for a 6-year-old fertilized and control plots of *P. taeda* (see

Table 3). The SETRES-II study site is adjacent to the SETRES experiment described in Ewers *et al.* (1998, 2001a,b). The stand, predominantly *Pinus taeda* L., was planted in 1993 at 1.5 m × 2.1 m spacing on an infertile, well-drained, sandy, siliceous, thermic Psammentic Hapludult soil (Wakulla series) with a water holding capacity of 12–14 cm in a 2 m profile. Foliar nutrient ratios are used to guide annual fertilizer applications aimed at maintaining a balanced and optimal supply of all nutrients in the fertilized plots, so as to stimulate rapid growth. The nitrogen treatment, approximately 11.2 g m⁻² per year as urea, supplemented as necessary with other nutrients is described in Albaugh *et al.* (1998). Using sapflux measurements, Ewers *et al.* (2001a,b) estimated canopy g_{ref} for the fertilized and control plots from the nearby site (SETRES) with similar soil–root–plant hydraulic characteristics as the Lai *et al.* (2002) fertilization study. The measured canopy g_{ref} increased 2.5-fold under an optimal fertilization regime. Using the measured leaf area index and g_{ref} (the latter, as demonstrated earlier, includes all stomatal responses except to vapour pressure deficit) we estimate the enhance-

Table 3. Measured L_{AI} and $V_{cmax,25}$ of *P. taeda* at SETRES-II (from Lai *et al.* 2002) after 6 years of nitrogen fertilization. The SETRES-II site is near the SETRES site whose ecophysiological and hydraulic parameters are described in Ewers *et al.* (2001a) and Hacke *et al.* (2000). The g_{ref} are from Ewers *et al.* (2000)

Variable	Control	Fertilized
L_{AI} (m ² m ⁻²)	1.65	3.51
$V_{cmax,25}$ (μmol m ⁻² s ⁻¹)	85.4	100.2
g_{ref} (mmol m ⁻² s ⁻¹)	50	125

ment in V_{cmax} to be: $\frac{V_{\text{cmax}}^{(f)}}{V_{\text{cmax}}^{(c)}} \approx \frac{1.65}{3.51} \times \frac{125}{50} = 1.18$ or about

18% enhancement, where $V_{\text{cmax}}^{(f)}$ and $V_{\text{cmax}}^{(c)}$ are the maximum carboxylation capacity for the fertilized and control stands, respectively. The gas-exchange measured $\frac{V_{\text{cmax}}^{(f)}}{V_{\text{cmax}}^{(c)}} = \frac{100.2}{85.4} = 1.17$, which closely matches the enhancement calculated above.

An immediate consequence of this approach is that older forests will have lower V_{cmax} when compared with younger forests because of the lower hydraulic conductances and g_{ref} of older and taller trees (e.g. Yoder *et al.* 1991; Saliendra *et al.* 1995; Hubbard *et al.* 1999; Schäfer *et al.* 2000). Furthermore, older forests typically have reduced leaf nitrogen; hence, it is expected that they also have a smaller V_{cmax} (Ellsworth 2000; Clearwater & Meinzer 2001; Lai *et al.* 2002). Both of these results (i.e. reduced V_{cmax} and $g_{\text{s,max}}$ with age) are consistent with the numerous observations that photosynthetic rates also declines with age even after a stand achieves an L_{AI} that remains approximately constant during that decline period (Ryan & Yoder 1997a, Ryan, Binkley & Fownes 1997b).

CONCLUSIONS

Simple equations describing water supply by the soil and roots to leaves, water loss through transpiration, stomatal conductance and photosynthesis, have led to an expression between V_{cmax} , mean intercellular CO_2 concentrations, leaf area index and the hydraulic conductance of the plant, G_{re} . The model predicts a strong, linear dependence of V_{cmax} on G_{re} which is independent of volumetric soil moisture contents, $\theta > 0.3$, and a non-linear, decreasing dependence in drier soils.

Intercellular CO_2 concentration, C_i , are shown to depend strongly on moisture content and atmospheric humidity deficit, plant hydraulic conductance and soil type. An equilibrium between maximum carbon demand by photosynthesis and maximum water supply by the soil leads to a unique long-term mean intercellular CO_2 concentration. The C_i at equilibrium can be thought of as a reference state to assess any shifts in hydraulic conductance of soil and plant and photosynthetic capacity. Where the long-term measured C_i/C_a (e.g. as determined by the carbon isotope discrimination method) is consistent with this equilibrium value and does not vary in time, then the ecophysiological and hydraulic properties are invariant and in equilibrium. A consequence of equilibrium as defined in this study, is an analytical method that can be used to estimate shifts in ecophysiological properties such as V_{cmax} based on shifts in hydraulic properties. Such understanding of the dynamics of V_{cmax} on time scales relevant to stand development is necessary to quantifying future terrestrial carbon cycling.

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